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C. Conley and P. Fife

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ABSTRACT

A generalized Morse index theory is used to study the existence of travelling wave solutions of a diffusion-reaction system of equations. The reaction system is assumed to be "close" to one which admits an attracting manifold of critical points. A scaling argument is used to see that the equations for travelling waves of the full system are then close to a system with a normally hyperbolic manifold of critical points.

Standard perturbation theorems are already available to study the behavior of solutions of the "perturbed" system which lie near the critical manifold in terms of a (derived) system of "slow" equations on the manifold itself. Here, another such theorem, dealing with aspects of the system which can be described in terms of isolated invariant sets, is proved. Specifically, it states that isolated invariant sets of the slow equations correspond to isolated invariant sets of the full system, and that the Morse index of the latter set is an n-fold suspension of that of the former where n is the number of unstable normal directions.

These theorems are applied to a standard continuous space-time natural selection-migration model for a diploid organism when the selective strength is weak. The selection is assumed to be determined by a single locus at which the number of available alleles is arbitrary, and the critical manifolds are found in this case.

The perturbation theorem is applied to a system with only two alleles in a situation where the existence of a travelling wave for the slow equation has long been known. The conclusion is that the full system also admits a corresponding travelling wave. The index theory is of use because the travelling wave itself is part of an isolated invariant set.

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SIGNIFICANCE AND EXPLANATION

Population of a given species can be classified in terms of the "alleles" at one or several chromosome loci. Natural selection may then give preference to some classes over the others. In some instances there may be two (or more) classes that are more "fit" than the classes near them (they are <u>locally</u> the fittest). However, if the population is distributed in a symmetric way so that one of these classes dominates in half the space and the other in the other half, and if "migration" is allowed, then one or the other class might take over. Thus the "fitness function" does not tell the complete story in such a situation.

In the mathematical model studied here the more complete picture is understood in terms of the travelling wave solutions of a diffusion-reaction system. The equations have the special feature that, in the absence of selection terms, they admit a full "manifold" of (neutrally) stable equilibria. This report shows how to use (Morse) index methods to study the travelling waves in the presence of this feature.

The responsibility for the wording and views expressed in this descriptive summary lies with MRC, and not with the authors of this report.

CRITICAL MANIFOLDS, TRAVELLING WAVES AND AN EXAMPLE FROM POPULATION GENETICS

C. Conlevy and P. Fife

§1. Introduction.

A critical manifold for a system of ordinary differential equations means a manifold of critical points. The system of equations from population genetics which is treated here admits such manifolds when no "selection" terms are present.

General perturbation theorems are available for the study of the equations with small selection terms added. In §2 a simple version of such a theorem, which is particularly adapted to the motivating question of this report, is proven.

The results of this report are applied to prove the existence of travelling wave solutions of the system of partial differential equations representing a standard continuous space-time natural selection-migration model for a diploid organism, when the selective strength is weak. Selection operates at a single locus with two alleles, so the system has three equations (one for each genotype); however most of our formalism applies to the multi-allele case. Underdominance, when the two homozygotes are fitter than the heterozygote, is assumed, since that is the case when a unique travelling wave front is expected.

The key step in the proof of the result is a scaling which presents the travelling wave equations as a small perturbation of a system with a critical manifold. The appropriate limiting problem on this manifold has been well studied and is known to have a unique solution.

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With the aid of the results of § 2, the main existence result is proved in § 4. The proof can be played back to a shooting argument or an "index" argument. Since the latter has been carried out in [1] the details are omitted here. However, a fairly detailed outline of the way in which the index arguments can be used is given even though the simplicity of the example treated doesn't really warrant it. The point is to set things up for later treatment of more complicated situations.

§ 2. Behavior of solutions near a critical manifold.

2.1. Critical Manifolds.

A. Definition.

Let

$$du/dt = U(u) \tag{1}$$

be a system of differential equations with u in $\mathbb{R}^n$. A critical manifold, $\mathfrak{m}$, for this system means a manifold of critical points (i.e. points at which $U = 0$).

The critical manifold is non-degerate at $u \in \mathfrak{m}$ if the matrix $\partial U/\partial u$ evaluated at u has, in addition to the zero eigenvalues corresponding to directions in $\mathfrak{m}$, only non-zero eigenvalues.

If these additional eigenvalues have only non-zero real parts, the manifold is called normally hyperbolic at u; if only negative real parts, attracting at u.

Though we will not use the fact, it is easy to see that the existence of an invariant manifold is inherited by the tangent equations:

B. Theorem: Suppose U is C^1; then to (1) there corresponds the system of tangent equations:

$$\begin{aligned} du/dt &= U(u) \\ dv/dt &= (\partial U/\partial u)\, v. \end{aligned} \tag{2}$$

For this system the set of points $\overline{\mathfrak{m}} \equiv \{(u, v) \mid u \in \mathfrak{m}$ and v is tangent to $\mathfrak{m}$ at $u\}$ is a critical manifold with twice the dimension of $\mathfrak{m}$.

If $\mathfrak{M}$ is non-degenerate, hyperbolic or attracting at u_0 then the same is true of $\bar{\mathfrak{M}}$ at points (u_0, v) in $\bar{\mathfrak{M}}$.

Proof. Since $U|\mathfrak{M} \equiv 0$, if $u \in \mathfrak{M}$ and v is tangent to $\mathfrak{M}$ then $U(u) = 0$ and $(\partial U/\partial u)v = 0$. Therefore, $\bar{\mathfrak{M}}$ is a critical manifold. The analogue of $\partial U/\partial u$ in the definition is the matrix

$$\begin{pmatrix} \partial U/\partial u & 0 \\ * & \partial U/\partial u \end{pmatrix}$$

where the $*$ refers to terms irrelevant to the present issue. The eigenvalues of this matrix are the same as those of $\partial U/\partial u$ and so the second statement of the theorem is true.

C. The existence of critical manifolds for (1) also implies existence of such for the "projectivized" tangent equation but a precise theorem requires a more refined hypothesis. Since it is not needed here, it is omitted.

The reason for mentioning the tangent and projectivized tangent equations is discussed in 2.3D.

2.2 A Parametrized Family of Equations.

The perturbation theorem concerns the smooth, one parameter family of equations

$$\dot{u} = U_\varepsilon(u, \varepsilon) = U_0(u) + \varepsilon U(u, \varepsilon) \quad \left(\dot{} = \frac{d}{dt} \right), \tag{3}$$

and in particular the behavior of solutions near a critical manifold which is assumed to exist when $\varepsilon = 0$.

Letting x denote coordinates in the manifold and y complementary coordinates, the equations can be written as:

$$(4)\qquad \begin{aligned} \dot{x} &= X_\ell(x)y + X_q(x,y) + \varepsilon X(x,y,\varepsilon) \\ \dot{y} &= Y_\ell(x)y + Y_q(x,y) + \varepsilon Y(x,y,\varepsilon) \end{aligned}$$

where X_ℓ and Y_ℓ are matrix valued functions of x, and X_q and Y_q are of order at least two in y. These terms come from U_0 while the last come from εU.

Now the critical manifold is non-degenerate at x if and only if $Y_\ell(x)$ is non-singular. If this non-degeneracy condition is satisfied for x in some compact subset, say N, of the critical manifold, then coordinates can be chosen so that $X_\ell(x) \equiv 0$ on N.

Namely, let $\tilde{x} = x - X_\ell(x)\, Y_\ell^{-1} y$. Then, computing modulo terms of order two in y or one in ε, there results:
$\dot{\tilde{x}} = \dot{x} - X_\ell Y_\ell^{-1} \dot{y} = X_\ell y - X_\ell Y_\ell^{-1} Y_\ell y = 0$. The equations (4) then assume the form:

$$(5)\qquad \begin{aligned} \dot{x} &= X_q(x,y) + \varepsilon X(x,y,\varepsilon) \\ \dot{y} &= Y_\ell(x)y + Y_q(x,y) + \varepsilon Y(x,y,\varepsilon), \end{aligned}$$

with X_q and Y_q of order at least two in y.

Assume now that the critical manifold is hyperbolic for points x in a compact set N. Then the y-coordinate can be modified if necessary so that for $x \in N$, $Y_\ell(x)$ has the form:

$$(6)\qquad Y_\ell(x) = \begin{pmatrix} Z_\ell(x) & 0 \\ 0 & W_\ell(x) \end{pmatrix}$$

where $Z_\ell(x)$ is negative definite and $W_\ell(x)$ is positive definite. Let $y = (z, w)$ where the decomposition corresponds to that of Y_ℓ and let Z_q, W_q and Z, W be the matching notation for Y_q and

Y. Then the equations have the form:

$$(7)\qquad \begin{aligned} \dot{x} &= X_q(x, y) + \varepsilon X(x, y, \varepsilon) \\ \dot{z} &= Z_\ell(x)z + Z_q(x, y) + \varepsilon Z(x, y, \varepsilon) \\ \dot{w} &= W_\ell(x)w + W_q(xy) + \varepsilon W(x, y, \varepsilon) \end{aligned} \quad .$$

The $\dim(z)$ will be called the number of *stable directions*; $\dim(w)$ the number of unstable ones.

2.3 Compact invariant sets near the critical manifold.

A. Theorem: Suppose the critical manifold $\mathfrak{m}$ is hyperbolic for all points in some compact set N. Then there is a neighborhood in u-space of the interior of N (rel. $\mathfrak{m}$) which is independent of ε and such that the distance from invariant sets in this neighborhood to points in $\mathfrak{m}$ is of order ε.

More specifically, suppose the critical manifold $\mathfrak{m} = \{u \mid u = (x, 0)\}$ of (5) is hyperbolic at points in the compact set $N \subset \mathfrak{m}$. Using the coordinates of (7), for $k > 0$ define $N(k) \equiv \{u = (x, z, w) \mid |z|, |w| \le k\}$.

Then there are positive constants ε_0, k_0 and k_1 such that: if $\varepsilon \le \varepsilon_0$ and S is an invariant set in $N(k_1)$, then S is in $N(\varepsilon k_0)$.

In fact, if $\varepsilon \le \varepsilon_0$, $k \in [\varepsilon k_0, k_1]$ and $u \in N(k)$, then whenever $|z| = k$, $|z|^\bullet < 0$ and whenever $|w| = k$, $|w|^\bullet > 0$.

Proof. The last sentence implies the previous one as follows. Assuming S is in $N(k_1)$, let k be the smallest number such that $S \subset N(k)$. Then (if S isn't empty) there must be a point of S at which $|z| = k$ or $|w| = k$. Now if k were in $[\varepsilon k_0, k_1]$ then either $|z|^\bullet < 0$ or $|w|^\bullet > 0$ — whichever is relevant — and it would follow that the solution leaves $N(k)$ in one or the other time direction. Therefore k cannot be in $[\varepsilon k_0, k_1]$. Since $k \le k_1$, it must be less than εk_0. Thus the last sentence implies the full theorem

Now let ε_0 and k_1' be positive constants such that the right hand sides of (7) are defined for $\varepsilon \le \varepsilon_0$ and $|z|, |w| \le k_1'$.

Let c_1 be a bound for $|Z|$ and $|W|$ for all $u \in N(k_1')$ and $\varepsilon \le \varepsilon_0$.

Choose k_0 so that $k_0^{-1}(2 + c_1)$ is a lower bound for the quadratic forms $-Z_\ell(x)$ and $W_\ell(x)$ whenever $x \in N$. Let c_0 be a bound for $|Z_q|/|y|^2$ and $|W_q|/|y|^2$ for all $u \in N(k_1')$. Define $k_1 = \min(k_1', 1/c_0 k_0)$. Now suppose $\varepsilon \le \varepsilon_0$, $k \in [\varepsilon k_0, k_1]$, $u \in N(k)$ and, say, $|z| = k$. Compute: $(\frac{1}{2}|z|^2)^\bullet = (z, Z_\ell z) + (z, Z_q) + \varepsilon(z, Z) \le -k_0^{-1}(2+c_1)|z|^2 + |z|\,|Z_q| + \varepsilon|z|\,|Z|$. Since $u \in N(k)$ and $|z| = k$, $|w| \le k$ and $|y|^2 \le 2k^2$. Therefore:

$$(\tfrac{1}{2}|z|^2)^\bullet \le |z|\,[-k_0^{-1}(2 + c_1)k + 2k^2 c_0 + \varepsilon c_1] =$$

$$= |z|\,[2k(-k_0^{-1} + k c_0) + c_0(-k_0^{-1} k + \varepsilon)] .$$

Now since $k \in [\varepsilon k_0, k_1]$, $-k_0^{-1}k + \varepsilon \leq 0$. Also, because $k_1 \leq 1/c_0 k_0$, $-k_0^{-1} + kc_0 \leq 0$. Furthermore at least one of these terms is negative, so $(\frac{1}{2}|z|^2|^{\bullet} < 0$.

If $|w| = k$, a similar computation shows that $(\frac{1}{2}|w|^2)^{\bullet} > 0$ and the theorem follows.

B. <u>Definition.</u> A non-degenerate isolating block for the differential equation.

$$(8) \qquad \dot{v} = f(v)$$

means a compact set B described in terms of a finite number of (smooth) functions $L_1, \ldots, L_m$ as $B \equiv \{v \mid L_i(v) \leq 0 \text{ for } i = 1, \ldots, m\}$. It is also required that if $v \in \partial B$, then for one of the defining L_i, $L_i(v) = 0$ and $\dot{L}_i(v) (= \nabla L \cdot f(v)) \neq 0$. If (this) $\dot{L}_i(v)$ is positive at v, v is called an exit point; if negative, v is an entrance point. (It is possible to be both an exit and an entrance point.)

Blocks are more generally defined in [1], page 55, lines 4 and 5.

C. Theorem: With reference to (5), let $X_s(x) \equiv X(x, 0, 0)$. Suppose B is a non-degenerate block for the equation

$$(9) \qquad \dot{x} = X_s(x).$$

and that $\mathfrak{m}$ is hyperbolic at points $u = (x, 0)$ with $x \in B$. Let k_0 be as in Theorem 2.3 A where the N of that theorem is replaced by B.

Then there exists $\varepsilon_1 > 0$ such that if $\varepsilon \leq \varepsilon_1$, the set $\bar{B} \equiv \{u = (x, z, w) \mid x \in B \text{ and } |z|, |w| \leq \varepsilon k_0\}$ is a block for (5).

The exit set of this block is the set of points $u = (x, y, z)$ with x in the exit set of B or $|w| = \varepsilon k_0$.

Proof: For the functions defining $\bar{B}$, take the $L_i (i = 1, \ldots, m)$ defining B, (but now considered as functions of $u = (x, z, w)$) together with $L_{m+1} = \varepsilon k_0 - |z|$ and $L_{m+2} = \varepsilon k_0 - |w|$.

Now given a boundary point of $\bar{B}$ at which $|z| = \varepsilon k_0$, the function L_{m+1} or L_{m+2} (resp.) is that required in the definition. Namely, by the last sentence of Theorem 2.3 A the derivative on the solution through the boundary point of the appropriate one of these is not zero.

Given a boundary point of $\bar{B}$ with both $|z|$ and $|w| \neq \varepsilon k_0$, the x-coordinate of this point is in the boundary of B. Let L_i be the function such that $L_i(x) = 0$ and $dL_i(X_s)(x) \neq 0$.

The derivative of L_i on solutions of (5) is given by $dL_i(X_q(x, y) + \varepsilon X(x, y, \varepsilon)) = \varepsilon dL_i(X_s(x)) + dL_i[X_q(x, y) + \varepsilon(X(x, y, \varepsilon) - X(x, 0, 0)]$. Now in $\bar{B}$, $|y|^2 \leq 2\varepsilon^2 k_0^2$. Since $X_q(x, y)$ is of order at least two in y and $X(x, y, \varepsilon) - X(x, 0, 0)$ is of order at least one in y, the terms in square brackets are of order at least two in ε. Because $dL_i(X_s(x)) \neq 0$ the derivative of L_i on solutions of (5) is non-zero <u>in a neighborhood</u> of $u = (x, y, z)$ provided ε is small enough. Covering the boundary of $\bar{B}$ with a finite number of such neighborhoods and taking ε_1 to be the least of the ε's, the result follows.

D. Remarks: The equation (9) of Theorem 2.3 C above provides (except for the change in time scale) the lowest order approximation for the behavior of the x-coordinates of solutions of (3) near $\mathfrak{m}$. Of course these coordinates change at rate (at most) ε since $\mathfrak{m}$ is a manifold of rest points of (3) when $\varepsilon = 0$.

Definition. The equation $x = X_s(x)$, considered as an equation on $\mathfrak{m}$, will be called the limit equation on $\mathfrak{m}$ (as $\varepsilon \to 0$).

Theorem 2.3 C states that any properties of this limit equation which can be described in terms of isolating blocks(or "local Liapounov functions" like the L_1) can be carried over to (3). In view of the remarks in 2.1B. and C., the same holds for properties describable in terms of isolating blocks for the tangent and projectivized tangent equations and their iterates.

There are several such properties: for example, the statement that (9) admits a compact hyperbolic invariant set in a given conjugacy class can be expressed in terms of blocks for the tangent and projectivised tangent equations. Thus, if $S \subset \mathfrak{m}$ is such an invariant set of the limit equation, then for small ε, (3) admits a compact hyperbolic invariant set conjugate to (and within $k_0 \varepsilon$ of) S. More specially, S might be a hyperbolic critical point or periodic orbit of (9), which then perturbs to an orbit of the same type for (3) - though of course the dimensions of the stable and unstable manifolds generally increase.

As another example, the usual hypothesis on a compact invariant manifold that allows a perturbation result preserving smoothness of order r can also be stated in terms of isolating blocks of an iterated tangent equation. Thus if $\mathfrak{m}' \subset \mathfrak{m}$ is a compact invariant C^r - manifold for (9) which satisfies this hypothesis then for small ε, (and assuming enough smoothness) (3) admits an invariant C^r- manifold homeomorphic to and near $\mathfrak{m}'$.

(It is more challenging to try to find a perturbable property <u>not</u> describable in terms of blocks.)

In a different direction, it is (also) well known that with a sequence of coordinate transformations, (9) can be replaced by better approximations for the behavior of the x-coordinates of those solutions in an invariant set S near $\mathfrak{m}$. In fact $\mathfrak{m}$ itself can be replaced by critical manifolds of the transformed equations which pass within $O(\varepsilon^n)$ of S. (In other words, uniform asymptotic expansions can be given for solutions in S.)

The use of Theorem 2.3 C in the setting of the Morse index is illustrated §3.4 B. In [3] a more general theorem about isolating neighborhoods for parametrized families of equations is proved. It can be used in connection with the Morse index in the same way.

2.4 Travelling waves.

A. The travelling wave equation.

The motivating problem of this report concerns the system of travelling wave equations associated to a partial differential equation of the form:

$$(10) \qquad \partial u/\partial t = \partial^2 u/\partial \xi^2 + U_0(u) + \sigma^2 U(u, \sigma).$$

The travelling wave equations are ordinary differential equations derived on assuming a solution of (10) in the form $u(t, \xi) = u(\xi - \sigma ct)$.

Letting $\tau = \xi - ct$, and $' = d/d\tau$ and dropping the tilde, these equations assume the form

$$(11) \qquad -\sigma c u' = u'' + U_0(u) + \sigma^2 U(u, \sigma).$$

We are interested in the case where, when $\sigma = 0$, the equations for the spatially independent solutions of (10) (i.e. the equations without the diffusion terms) admit a non-degenerate critical manifold. As in 2.2, this implies there is a coordinate transformation $u \longmapsto (x, y)$ such that these equations, namely

$$(12) \qquad \dot{u} = U_0(u) + \sigma^2 U(u, \sigma),$$

transform to

$$(13) \qquad \begin{aligned} \dot{x} &= X_q(x, y) + \sigma^2 X(x, y, \sigma) \\ \dot{y} &= Y_\ell(x) y + Y_q(x, y) + \sigma^2 (x, y, \sigma) \end{aligned}$$

where X_q and Y_q have order at least two in y.

Now, in general, the coordinate transformation $u \longrightarrow \varphi(z)$ transforms (12) to:

$$(14) \qquad z' = (d\varphi)^{-1} U_o(u(z)) + \sigma^2 d\varphi^{-1} U(u, \sigma)$$

where $d\varphi$ is the Jacobean matrix of the transformation. Therefore, if $z = (x, y)$ and φ is the transformation $u \longrightarrow (x, y)$ above, then $(d\varphi)^{-1} U_o(u(z)) + \sigma^2 d\varphi^{-1} U(u, \sigma)$ is the right hand side of (13).

Applying the transformation $u = \varphi(z)$ to (11), one computes:

$$u' = d\varphi(z'),$$

$$u'' = d^2\varphi(z') + d\varphi(z'') \quad \text{and, from (11),}$$

$$(15) \qquad -\sigma c\, d\varphi(z') = d^2\varphi(z') + d\varphi(z'') + U_o(u(z)) + \sigma^2 U(u(z), \sigma), \quad \text{or}$$

$$z'' = -\sigma c\, z' - (d\varphi)^{-1} U_o(u(z)) - \sigma^2 (d\varphi)^{-1} U(u(z), \sigma) - d\varphi^{-1}(d^2\varphi(z')).$$

Now let $z = (x, \sigma y)$ (rather than (x, y)). Then the terms $-d\varphi^{-1} U_o(u(z)) - \sigma^2 d\varphi^{-1} U(u(z), \sigma)$ take the form (from the right hand side of (13) with the noted modification):

$$(16) \qquad \begin{aligned} &X_q(x, \sigma y) + \sigma^2 X(x, \sigma y, \sigma) \\ &Y_\ell(x)\, \sigma y + Y_q(x, \sigma y) + \sigma^2 Y(x, \sigma y, \sigma) \end{aligned}$$

In particular, excepting $Y_\ell(x)\,\sigma y$, these terms are of order at least two in σ and, when $y = 0$, the x-term reduces to $\sigma^2 X(x, 0, 0)$; this is, in the notation of Theorem 2.3 C, $X_s(x)$.

On introducing ξ and η (corresponding to x and y) by $(\sigma\xi, \sigma\eta) = z'$, the last equation of (14) now leads to the system:

$$
(17)\qquad
\begin{aligned}
x' &= \sigma\xi \\
y' &= \eta \\
\xi' &= -\sigma c\,\xi - \sigma^{-1}X_q(x, \sigma y) + \sigma X(x, \sigma y, \sigma) - \sigma\Phi(\xi, \eta) \\
\eta' &= -\sigma c\,\eta - Y_\ell(x)y + \sigma^{-1}Y_q(x, \sigma y) + \sigma Y(x, \sigma y, \sigma) - \sigma\psi(\xi, \eta)
\end{aligned}
$$

where $d\varphi^{-1}(d^2\varphi(\sigma^{-1}z'))$ is decomposed into $\Phi(\xi, \eta)$ and $\psi(\xi, \eta)$ in accordance with the decomposition $\sigma^{-1}z' = (\xi, \eta)$. ($\Phi$ and ψ also depend on x and y of course; they are quadratic in ξ and η.)

B. Theorem: Suppose the equations (12) for the spatially independent solutions of (10), that is of $\partial u/\partial t = \partial^2 u/\partial \xi^2 + U_0(u) + \sigma^2 U(u, \sigma)$, admit a non-degenerate critical manifold, $\mathfrak{m}$, when $\sigma = 0$. Then the same is true of the equations for travelling waves if they are appropriately scaled (as they are above).

More specifically, when $\sigma = 0$, the equations (17) admit the critical manifold $\bar{\mathfrak{m}} = \{(x, y, \xi, \eta) \mid y = \eta = 0\}$. Coordinates on $\bar{\mathfrak{m}}$ are given by (x, ξ) and the limit equations on $\bar{\mathfrak{m}}$ are given by:

$$
(18)\qquad
\begin{aligned}
x' &= \xi \\
\xi' &= -c\xi - X_s(x) - \Phi(\xi, 0),
\end{aligned}
$$

where the limit equations on $\mathfrak{m}$ are:

$$
(19)\qquad x' = X_s(x).
$$

The critical manifold, $\overline{\mathfrak{m}}$, is non-degenerate if $\mathfrak{m}$ is, and is hyperbolic if $\mathfrak{m}$ is attracting. (If the linearized equations for $\mathfrak{m}$ have a real positive eigenvalue, $\overline{\mathfrak{m}}$ is not hyperbolic). If $\mathfrak{m}$ has n stable directions, $\overline{\mathfrak{m}}$ has n unstable ones.

Proof: On setting $\sigma = y = \eta = 0$, the right hand side of (17) vanishes (recall that X_q and Y_q are of order 2 in their second variable so $\sigma^{-1} X_q(x, \sigma y)$ and $\sigma^{-1} Y_q(x, \sigma y)$ are of order one in σ). The relevant portion of the matrix for the linearized equations is

$$(20) \qquad \frac{\partial (y', \eta')}{\partial (y, \eta)} = \begin{pmatrix} 0 & I \\ Y_\ell(x) & 0 \end{pmatrix} .$$

It is non-degenerate if $Y_\ell(x)$ is and it's eigenvalues are the square roots of those of $Y_\ell(x)$.

Setting $y = \eta = 0$ and taking the terms of order σ in the x, ξ equations gives (18). The equations (19) come on taking the lowest order terms in the corresponding equations for (12). These are of order σ^2.

§ 3. Some Equations from Mathematical Population Genetics.

2.1 The Growth Equations.

As we consider continuous-time models of natural selection at a single gene locus. Equation (21) and equations analogous, in varying degrees, to those in Sections 3.1B, C can be found in a number of works; see, for example, [4-8].

There is supposed to be a population with a total of T individuals which is classified according to which two of n possible "alleles" appear at a particular gene locus. The number of alleles of type A_i is $2N_i$, and $u_{ij}(= u_{ji})$ is the number of ordered A_iA_j genotypes. Consequently, $N_i = \Sigma_j u_{ij}$ and $T = \Sigma_i N_i = \Sigma_{ij} u_{ij}$.

The growth equations are assumed to have the form:

$$\dot{u}_{ij} = \beta T^{-1} N_i N_j - \delta u_{ij} + \varepsilon g_{ij}, \tag{21}$$

where β and δ can be taken to be (positive) functions of u and g_{ij} is some function of u (frequently a constant multiple of u_{ij}). In particular, the birth rate, $\beta T^{-1} N_i N_j$, of the u_{ij} types is proportional to the product of the numbers of individuals with the i^{th} and j^{th} alleles (respectively). This is the "random mating" hypothesis. The (essential) restriction that β and the exponential death rate, δ, do not vary from equation to equation corresponds to an assumption that differences in fertility and survival ability, accounted for in the g_{ij} terms, are small enough to be treated as a perturbation, hence, the parameter ε. These same terms may account for small deviations from random mating and for the systematic introduction into the population, through mutation or otherwise, of small numbers of the various genotypes.

B. Random Mating and the Hardy-Weinberg Surface.

In view of the random mating hypothesis it is easy to guess that (if $\varepsilon = 0$) the population might tend to a state where $u_{ij} = T^{-1} N_i N_j$ (the alleles should be independently distributed). This suggests introducing the functions

$$h_{ij} = T^{-1} N_i N_j - u_{ij}. \tag{22}$$

Writing u for u_{ij} etc. and ρ for $\beta - \delta$ (the effective exponential growth rate) the equations become:

$$\dot{u} = \rho u + \beta h + \varepsilon g. \tag{23}$$

The derivative of h along solutions of this equation is $\dot{h} = \rho dh(u) + \beta dh(h) + \varepsilon dh(g)$. Since h is homogeneous of degree 1, the first term on the right is just ρh. Also, since $\Sigma_j h_{ij} = 0$, $N_i = \Sigma_j u_{ij}$ and $T = \Sigma_j N_j$ do not change under displacements in the h direction; therefore $dh(h) = dh(-u_{ij}) = -h$.

Recalling that $\rho - \beta = -\delta$, this gives:

$$\dot{h} = -\delta h + \varepsilon dh(g). \tag{24}$$

Of course the death rate, δ, is positive, so if $\varepsilon = 0$ h tends to zero exponentially.

The surface defined by $h = 0$ is called here the Hardy-Weinberg surface. It is n-dimensional and coordinates on it are supplied by the vector $N = (N_1, \ldots, N_n)$. In fact, if $\hat{h}$ denotes the set of $(n^2 - n)$ h_{ij}

with $i \neq j$, then when $T \neq 0$ the transformation $u \longrightarrow (N, \hat{h})$ is well defined and invertible and has Jacobean one.

Namely, from the definition (22), $h_{ij} = T^{-1} N_i N_j - u_{ij}$, it follows that $u_{ij} = T^{-1} N_i N_j - h_{ij}$ so that N and $\hat{h}$ determine the u_{ij} with $i \neq j$. Then from $N_i = \Sigma_j u_{ij}$ one can determine u_{ii}.

To compute the Jacobean, observe that $dN_1 \wedge \ldots \wedge dN_n \wedge dh_{ij}$ must be the same as $dN_1 \wedge \ldots \wedge dN_n \wedge du_{ij}$ since h_{ij} and u_{ij} differ by a function of the N's. Then from $N_i = \Sigma_j u_{ij}$ it follows that $dN_1 \wedge \ldots \wedge dN_n \wedge (\bigwedge_{i \neq j} du_{ij}) = \bigwedge_{i,j} du_{ij}$ since the terms in N_i of the form du_{ij} with $i \neq j$ already appear in the product $\bigwedge_{i \neq j} du_{ij}$. The results follows.

C. Critical Manifolds.

On this Hardy-Weinberg surface, the equations (with $\varepsilon = 0$) are just $\dot{u} = \rho u$. Therefore the zero's of the effective growth rate, ρ, provide critical points. The growth rate is obviously positive for some values of u, and is negative if u is so large that the environment can not support the total population. Therefore the Hardy-Weinberg surface must be separated by a set of points where $\rho = 0$. This set is assumed to be a manifold, and is therefore an $n-1$ dimensional one.

It has already been seen (from (24)) that (when $\varepsilon = 0$), this manifold is attracting in the $n(n-1)/2$ independent directions corresponding to the h_{ij} with $i \neq j$. The situation in the remaining direction depends on the derivative of ρ.

An easy case to treat is that where ρ depends only on the total population, T, and has a zero at some critical value T_0. Then part of the critical manifold, $\mathfrak{m}$, is the set $\{u \mid h_{ij} = 0; \quad T = T_0\}$. Coordinates in this manifold are supplied by the gene frequencies:

$$P_i = N_i/T. \tag{25}$$

Now define coordinates P, and t by:

$$\begin{aligned} P &= (P_1, \ldots, P_n) \\ t &= T - T_0 \end{aligned} \tag{26}$$

and define G_i, G, the constant λ and the function $r(t)$ (of order two in t as $t \to 0$) by:

$$\begin{aligned} G_i &= \Sigma_j \, g_{ij} \\ G &= \Sigma_i \, G_i \\ \lambda &= -[\rho(T_0+t)(T_0+t)]'(T_0) \quad \text{and} \\ r(t) &= \rho(T_0+t)(T_0+t) + \lambda t. \end{aligned} \tag{27}$$

Then the equations (21) assume the form:

$$\dot{P}_i = \varepsilon(T_0 + t)^{-1}[G_i - G P_i]$$

$$(28) \qquad \dot{t} = -\lambda t + r(t) + \varepsilon G$$

$$\dot{h} = -\delta h + \varepsilon d h(g) .$$

To see this add (21) over j to get $\dot{N}_i = \rho N + \varepsilon G_i$ and then over i to get $\dot{T} = \rho T + \varepsilon G$. Then $\dot{P} = (T^{-1} N)^{\bullet} = \varepsilon T^{-1}[G_i - GP_i]$ as required. The equation for t comes from (26) and (27) with $\dot{t} = \dot{T} = \rho(T) T + \varepsilon G$. That for h comes from (24). The equations for h_{ii} are redundant of course and h should be interpreted as the h_{ij} with $i \neq j$, i.e. $\hat{h}$. Observe that the equations (28) have the form of (5) with P replacing x and $(t, \hat{h})$ replacing y. The analogue of Y_ℓ is a diagonal matrix with a $-\lambda$ on the diagonal and remaining diagonal entries equal to $-\delta$. The analogue of X_q is zero and that of Y_q is $r(t)$.

It will be assumed that $\lambda > 0$ so this critical manifold is attracting.

The limit equations on the critical manifold $\mathfrak{m} \equiv \{P, t, \hat{h} \mid t = \hat{h} = 0\}$ are given by:

$$(29) \qquad \dot{P}_i = (G_i - G P_i)/T_0 .$$

With appropriate choice of g_{ij}, these are the well-known Fisher equations.

D. The Travelling wave equation.

The travelling wave equations associated to (23) are (defining v by the equation):

$$(30)\qquad \begin{aligned} u' &= v \\ v' &= -\sigma c v - \rho u - \beta h - \sigma^2 g, \end{aligned}$$

where ε has been replaced by σ^2 and the wave velocity is equal to σc.

The equations in the coordinates $(P, t, \hat{h})$ and their derivatives could be derived from the general form (17) or, since they are the only ones required, those for P and $Q = \sigma^{-1} P'$ can be computed directly as follows. Defining $t' = T' = \Sigma_{ij} v_{ij}$ to be σw there follows $\sigma w' = \Sigma_{ij} v'_{ij} = -\sigma^2 c w - \rho T - \sigma^2 G$. Then $N_i' = (T P_i)' = \sigma w P_i + \sigma T Q_i$. It then follows that $N_i'' = \sigma w' P_i + 2\sigma^2 w Q_i + \sigma T Q_i'$. Rearranging and using the above expression for $\sigma w'$ gives $Q_i' = (\sigma T)^{-1}[N_i'' + \sigma^2 c w P_i + \rho T P_i + \sigma^2 G P_i - 2\sigma^2 w Q_i]$.

Now using $\Sigma_j v_{ij} = N_i'$ and adding the second equation of (30) over j gives $N_i'' = -\sigma c N_i' - \rho T P_i - \sigma^2 G_i$. Using $N_i' = \sigma w P_i + \sigma T Q_i$ there results $N_i'' = -\sigma^2 c w P_i + \sigma^2 c T Q_i - \rho T P_i - \sigma^2 G_i$.

Substituting this last expression for N_i'' into the preceding equation for Q_i', there follows: $Q_i' = (\sigma T)^{-1}[-\sigma^2 c T Q_i - \sigma^2 G_i + \sigma^2 G P_i - 2\sigma^2 w Q_i]$. Thus the equations for P and Q are:

$$(31)\qquad \begin{aligned} P_i' &= \sigma Q_i \\ Q_i' &= -\sigma c Q_i - \sigma T^{-1}[G_i - G P_i] - 2\sigma T^{-1} w Q_i . \end{aligned}$$

These are the analogues of the equations for x and ξ in (18). However, it should be noted that there should really be only $2n-2$ equations in (31) since $\Sigma_i P_i = 1$ and consequently $\Sigma_i Q_i = 0$.

The critical manifold for the travelling wave equations (23) with $\varepsilon = 0$ is the manifold of points where $t = 0$ $(T = T_0)$, $w = 0$ and $h = h' = 0$. The limiting equations on this manifold are obtained by setting these variables equal to zero in (31) and taking the first order terms in σ. This gives:

$$
\begin{aligned}
P'_i &= Q_i \\
Q'_i &= -cQ_i - (G_i - GP_i)/T_0
\end{aligned}
\tag{32}
$$

Now the critical manifold for (28) is obviously attracting since $\lambda > 0$ with $n(n-1)/2 + 1$ stable directions assuming $u_{ij} = u_{ji}$. By theorem 2.4 B the corresponding one for (30) is hyperbolic with $n(n-1)/2 + 1$ unstable directions. Therefore (by 2.3 C) blocks for (32) carry over to blocks for (30).

In the following example, this will be used to prove the existence of a travelling wave for (30) from the (known) existence of such a wave for (32).

3.2 An Example.

A. The easiest example is that when $n = 2$ and $g_{ij} = \delta^1_{ij} u_{ij} + \delta^2_{ij} T P_i P_j$ (the first term representing a perturbation of the death rate, and the second a perturbation to the birth rate). Since $P_1 = 1 - P_2$ and $Q_1 = -Q_2$, only one pair of the equations in (3.2) is needed.

On the Hardy-Weinberg surface, $u_{ij} = TP_iP_j$ and on the critical manifold $T = T_0$. Therefore **setting** $\delta_{ij} = \delta_{ij}^1 + \delta_{ij}^2$ and taking $\delta_{12} = \delta_{21}$, we have

$$(G_1 - GP_1)/T_0 = P_1[\delta_1 \; P_1 \;\; \delta_{12} P_2 - \delta_{11}P_1^2 - 2\,\delta_{12} P_1 P_2 - \delta_{22}P_2^2] .$$

This last expression is a function of P_1 alone, since $P_2 = 1 - P_1$. It vanishes when $P_1 = 0$ or 1, and when the δ_{ij} are constant, it is cubic with third root

$$a = (\delta_{22} - \delta_{12})/(\delta_{11} + 2\delta_{12} + \delta_{22}) .$$

The quantities $1 + \delta_{ij}$ are called the fitnesses of the three genotypes. The case we shall be especially interested in is the "underdominant" case $\delta_{11} > \delta_{12}$, $\delta_{22} > \delta_{12}$.

Normalizing the δ_{ij} so that $\delta_{12} = 0$ and dropping the subscript, (31) (for P_1, Q_1) takes the form

$$\begin{aligned} dP/d\tau &= Q \\ dQ/d\tau &= -cQ - P(1 - P)(P - a) \end{aligned} \tag{33}$$

with $A = \delta_{22}/(\delta_{11} + \delta_{22})$.

B. These equations have been treated by several authors (e.g. [9-13]). Our aim is to use Theorem 2.3C to "lift" the results to the corresponding equation for the u_{ij}, or, more specifically, to prove:

<u>Theorem</u>. Let $u = (u_{ij})$ and $v = (v_{ij})$ with $i, j = 1, 2$. Let $N_i = \Sigma_j u_{ij}$ and $T = \Sigma_{ij} u_{ij}$. Let $\rho = \rho(T)$ and $\beta = \beta(T)$ be differentiable functions of T with β and $\beta - \rho$ both positive when T is positive. Let $h = (h_{ij}) = (T^{-1} N_i N_j - u_{ij})$

and let $g = g_{ij}$ be functions of u which reduce to the form $\delta_{ij}(T)\, u_{ij}$ when $h = 0$. Let σ and ρ be real parameters.

Assume that for some $T_0 > 0$, $\rho(T_0) = 0$ and $[d\rho/dT](T_0) < 0$. Also assume that $\delta_{12}(T_0) = \delta_{21}(T_0) = 0$ and $\delta_{11}(T_0) > \delta_{22}(T_0) > 0$ (under dominance). Then there is a $\sigma_0 > 0$ such that to each $\sigma < \sigma_0$ there corresponds a $c^* < 0$ such that if $c = c^*(\sigma)$, the equations

$$(34) \qquad \begin{aligned} du/d\tau &= v \\ dv/d\tau &= -\sigma c v - \rho u - \beta h - \sigma^2 g \end{aligned}$$

admit a non-constant solution $(u_\sigma(\tau),\ v_\sigma(\tau))$ which tends to distinct rest points as τ tends to minus or plus infinity.

On this solution $T = T_0 + O(\sigma)$ and the limits of u at minus and plus infinity (respectively) are given to order σ by:

$$(35) \qquad \begin{pmatrix} 0 & 0 \\ 0 & T_0 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} T_0 & 0 \\ 0 & 0 \end{pmatrix}.$$

With $P = T^{-1}(u_{11} + u_{12})$ the function $P_\sigma(\tau)$ corresponding to the above solution converges as $\sigma \to 0$ to a solution of the equation (33) which tends to the rest points $(0, 0)$ and $(1, 0)$ as τ tends to minus or plus infinity respectively. (Of course $c^*(\sigma)$ must also converge to a value of c for which such a solution exists).

<u>Proof:</u> The proof of this theorem could be phrased in terms of the "shooting method" since it is quite easy to construct the necessary blocks explicitly.

In fact, referring to (33) and the function H given in 3.3A, for all negative values of c the set

$$B \equiv \{(P, Q) \mid -\varepsilon \le P \le 1 + \varepsilon;\ H(a, 0) + \varepsilon \le H(P, Q) \le H(1, 0) + \varepsilon\}$$

is a block; it corresponds to the shaded region in Figure 1. It is easily seen that for c close to zero the branch of the unstable manifold of the rest point $(0, 0)$ leaves the block as indicated by the solid curve, and for c large it leaves as indicated by the dashed curve. It follows that for some value of c it goes to the rest point $(1, 0)$.

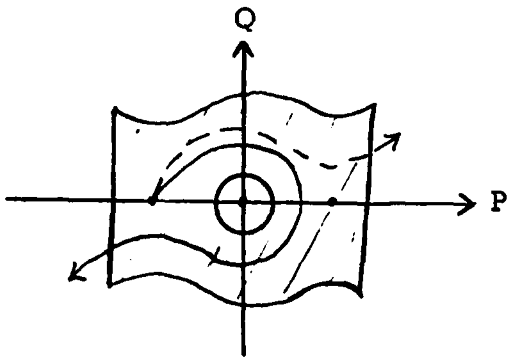

Fig. 1

Now using Theorem 2.3 C, this block corresponds to one for (3.4) and a similar "shooting argument" might be constructed.

Instead, the proof here will be based on the general facts about the Morse index of isolated invariant sets; this is to illustrate the use of this machinery and to set things up for a treatment of more complicated examples. Of course the same features enter the proof, but the index approach is probably easier to implement in general, particularly when it is difficult to construct blocks (or Ważewski sets, or local Liapounov functions...) explicitly. On the other hand, the index argument rests on a fairly large body of abstract definitions and theorems. The following description of which (without proofs) is already longer than a direct proof for this example would be. In 3.3 A, B and C and 3.4 B and C remarks pertinent to the example are more. In 3.5 a general theorem for travelling wave equations is given. Finally in 3.6 it is shown how the machinery works in the example.

3.3 Facts about (33).

A. Lemma If $c < 0$ the function $H(P, Q) = Q^2/2 - P^4/4 + (1+a)P^3/3 - aP^2/2$ is strictly increasing on non-constant solutions of (33). Consequently every bounded solution tends to a rest point in forward and backward time and the two rest points so determined are distinct.

There are three rest points for the equation; namely, $(a, 0)$, $(0, 0)$ and $(1, 0)$. The values of H at these three points are (respectively) $a^3(a-2)/12$, 0 and $(1-2a)/12$ and increase strictly in the order given when $0 < a < 1/2$ (as is assumed).

The set of bounded solutions is compact and in fact for all c is contained in the set $\{(P, Q) \mid 0 \leq P \leq 1;\ a^3(a-2)/12 \leq H \leq (1-2a)/12\}$.

Proof: In terms of H, the second equation of (33) is $dQ/d\tau = -cQ - \partial H/\partial P$. This makes it easy to see that, on solution, $dH/d\tau = -cQ^2$ and from there that H is strictly decreasing on non-constant solutions. The statement concerning the asymptotic behavior of the solutions now follows from well-known general facts about gradient-like equations (e.g. see [1], Ch. I, §6 p. 12 et seq.).

Since the equation is gradient-like with respect to H, the easily computed values of H at the critical points provide bounds for H on the set of bounded solutions. The bounds on P come from the fact that critical points of $P(\tau)$ are strict maxima if $P < 0$ and strict minima if $P > 1$ (cf. [1], Ch. II §4.3 C p. 31 for a more general result).

B. Lemma There is a constant k such that if $|c| \leq k$ then the rest point $(1,0)$ is a component of the set of bounded solutions of (35).

Proof: The point is obviously a component of the set of bounded solutions when $c = 0$ (when H is constant on solutions and the set of bounded solutions is easily pictured). Because it is compact, the set of bounded solutions depends upper semi-continuously on c. Because $(1, 0)$ is a hyperbolic rest point no new bounded solutions are created near this point when c changes a little. Therefore, it remains a component for $|c|$ small.

C. Lemma The equation

$$P' = P(1-P)(P-a) \tag{36}$$

is gradient-like with respect to the function $P^4/4 - (1+a)P^3/3 + aP^2/2$ and has critical points at 0, a and $1-a$.

For $0 < \varepsilon < a$, the interval $[a-\varepsilon, 1+\varepsilon]$ is an isolating block with exit set $\{a-\varepsilon\}$. It contains the two rest points a and 1.

Proof: Trivial.

3.4 <u>Interpretation of the previous Lemmas as statements about Morse decompositions.</u>

A. To conclude the proof the notions of attractors, Morse decompositions, the homotopy index and connection maps are used. An attractor relative to a compact invariant set, S, means a compact invariant subset which is the ω-limit set of a neighborhood of itself (Definition 5.1, p. 32 Ch. II, [1]). A Morse decomposition, $D = \{M_1, M_2, \ldots, M_n\}$, of S is derived from an increasing sequence $\phi = A_1, \ldots, A_n = S$ of attractors relative to S; namely, M_j is the maximal compact invariant set in $A_j \setminus A_{j-1}$ (Definition 7.1, p. 40, Ch. II, [1]). To each Morse set M_j there corresponds an index, h_j which takes the form of the homotopy type of a pointed space (Definition 5.1 and 5.2, pp. 51-52, Ch. III, [1]). To a pair of adjacent Morse sets, M_j, M_{j+1} in a decomposition there corresponds a connection map, c from h_{j+1} to the suspension of h_j (7.2, 7.3 pp. 61-62, Ch. III, [1]). All of these objects are "stable" under small perturbation (5.3 C, p. 35, Ch. II, Thm. 1.4 p. 67, Thm. 2.5, p. 70 and Thm. 3.1, p. 72, Ch. IV, [1]).

The application to the present problem goes as follows.

B. <u>Lemma</u> By Lemma 3.3 A with 7.1 C, p. 40, Ch. II of [1], $\bar{D} = \{(1,0), (0,0), (a,0)\}$ is a Morse decomposition of the set of bounded solutions of (33) for all values of c.

Furthermore, if there is no solution running from $(0,0)$ to $(1,0)$ $D = \{(0,0), (1,0), (a,0)\}$ is also a Morse decomposition

(7.1 C of [1] again). In particular, Lemma 3.3 B says no bounded solution runs to $(1, 0)$, so D is a Morse decomposition for small negative c.

Also, Lemma 3.3 B with Theorem 7.2 C, p. 62 of [1] implies the connection map from $h((a, 0))$ to the suspension of $h((1, 0))$ is trivial.

C. Lemma By Lemma 3.3 C, $D' = \{0, 1, a\}$ is a Morse decomposition of the set of bounded solutions of (36). Since $[a - \varepsilon, 1 + \varepsilon]$ can be deformed to its exit set $\{a - \varepsilon\}$ it has index $\overline{0}$ (cf. [1], bottom of p. 6 and top of p. 7). From (1), 7.2 B p. 62 Ch. III of [1], it then follows that the connection map from $h(a)$ to $h(1)$ is an isomorphism. Since $h(1) = \overline{1}$ (cf. middle p. 6, Ch. I of [1]) this connection map cannot be trivial.

3.5 Three more abstract theorems.

The idea now is to "lift" the Morse decompositions of 3.4 A and 3.4 B up to the equation (34) using Theorem 2.3 C or rather its following consequence (see Definition 3.2, Ch. III p. 45 of [1] for the definition of isolated invariant set and isolating neighborhood, and 5.2, Ch. III, p. 51 for the index).

A. Theorem: Let $\mathfrak{m}$ be a critical manifold for the equation

$$(37) \qquad \dot{u} = U_0(u, \varepsilon) + \varepsilon U(u, \varepsilon) \qquad (\dot{} = \frac{d}{dt})$$

when $\varepsilon = 0$, and let S be an isolated invariant set of the limit equation on $\mathfrak{m}$ such that $\mathfrak{m}$ is hyperbolic at points of S. Then any neighborhood of S in u-space contains a compact neighborhood $\bar{N}$ such that for small enough ε, $\bar{N}$ is an isolating neighborhood for (37). The corresponding family of isolated invariant sets will be denoted $S(\varepsilon)$.

If S is contractible in a subset of $\mathfrak{m}$ consisting of points at which $\mathfrak{m}$ is hyperbolic, then the index of sets in N is the product of that of S with a pointed r-sphere where r is the number of eigenvalues with positive real part of the matrix $\partial U/\partial u$ evaluated at any point of S, or in other words the number of unstable directions of $\mathfrak{m}$ in N.

The family $S(\varepsilon)$, will be called an r-fold extension of S.

Proof: This could be played back to Theorem 2.3C., or argued directly as follows. Let $\mathfrak{u}$ be a neighborhood of S in u-space. Since $\mathfrak{m}$ is hyperbolic at points of S, there is an isolating neighborhood N, of S (as an isolated invariant set of the limit equation) in $\mathfrak{m} \cap \mathfrak{u}$ such that $\mathfrak{m}$ is hyperbolic at points in N. Then for small enough k, the set $N(k)$ of Theorem 2.3 A is contained in $\mathfrak{u}$. For small enough ε it can be shown to be an isolating neighborhood for (37) as follows. Suppose given a solution which stays in $N(k)$ for all time; the thing to be shown is that this solution does not pass through a boundary point of $N(k)$. Now by Theorem 2.3 A, it lies within $O(\varepsilon)$ of $\mathfrak{m}$. Therefore, if ε is small, it closely follows solutions of the limit equation. Also, if ε is small enough, the y coordinate of the solution is smaller than k.

Therefore if the solution were to pass through a boundary point of $N(k)$ it would have to be one whose x-coordinate is in the boundary of N. Then the corresponding solution of the limit equation leaves N (because N is an isolating neighborhood of the limit equation). But then the given solution would have to follow it out of $N(k)$ which is a contradiction. This proves $N(k)$ is an isolating neighborhood of (37) if ε is small enough (in [3] there is a substantial generalization of this argument).

To compute the index of $S(\varepsilon)$, a block for S is chosen and then, by Theorem 2.3 C a block for $S(\varepsilon)$ (ε small). If S is contractible in a subset of $\mathfrak{m}$ at points in which $\mathfrak{m}$ is hyperbolic, then the block for $S(\varepsilon)$ can be deformed to the product of the given one for S and a block for a hyperbolic rest point whose unstable manifold is the number of eigenvalues with positive real part of $\partial U/\partial u$ evaluated at a point of S. This implies the statement about the index of S_ε (cf. §4, Ch. I of [1]).

B. <u>Theorem</u>: With the hypothesis of Theorem 3.5 A, suppose $D = \{M_1, \ldots, M_n\}$ is a Morse decomposition of S. Then $D(\varepsilon) \equiv \{M_1(\varepsilon), \ldots, M_n(\varepsilon)\}$ with the $M_i(\varepsilon)$ the r-fold extensions of M_i, is a Morse decomposition of $S(\varepsilon)$ for small enough ε. Furthermore the connection maps from $h(M_{j+1}(\varepsilon)$ to the suspension of $h(M_j(\varepsilon))$ are the r-fold suspensions of the corresponding maps for D.

Proof: This is a straightforward consequence of the definitions and the preceding theorem.

The next theorem is the result initiating §3, p. 81 of [2]*. It is included here for completeness and because it can be played back to critical manifolds as follows.

C. Theorem Let $D = \{M_1, \ldots, M_n\}$ be a Morse decomposition of an isolated invariant set S of the equation

$$\dot{u} = f(u). \tag{38}$$

where $u \in \mathbb{R}^r$. Then for large c, S and D admit r-fold extensions to the equation

$$\begin{aligned} u' &= v \\ v' &= -cv - f(u) \end{aligned} \tag{39}$$

which are obtained by realizing (38) as the limit equation for a critical manifold of a transformed version of (39), namely:

$$\begin{aligned} u' &= \varepsilon f(u) + \varepsilon w \\ w' &= w - \varepsilon f'(u)w - \varepsilon f'(u) f(u). \end{aligned} \tag{40}$$

This critical manifold has $\dim(u)$ unstable directions.

Proof: With $\varepsilon = 0$, the equations (40) become $u' = 0$, $w' = -w$ and so admit $\mathfrak{m} = \{(u, w) \mid w = 0\}$ as a critical manifold. The limit

*The function $f(v)$ introduced on page 80 of [2] can be taken to be $v(1-v)(v-a)$ with $0 < a < \frac{1}{2}$.

equation is $u' = f(u)$. Therefore 3.5 A and B apply.

The equation (40) transforms to 39 on setting $\varepsilon = c^{-2}$, changing the time scale by multiplying the right-hand sides by $-c$, and setting $w = -cv - f(u)$.

3.6 The conclusion of the proof.

Using Theorem 3.5 B and Lemma 3.4 B the Morse decomposition $\overline{D} = \{(1, 0), (0, 0), (a, 0)\}$ of the set S of bounded solutions of (33) extends to a decomposition $\overline{D}(\sigma)$ of the extension $S(\sigma)$ of S to (34). It is an elementary fact that the extensions of the (non-degenerate) rest points $(1, 0)(0, 0)$ and $(a, 0)$ are again rest points (as well as Morse sets). These Morse sets will be denoted respectively by $M_1(\sigma)$, $M_0(\sigma)$ and $M_a(\sigma)$.

By 7.1C, p. 40, Ch. II of [1], so long as there is no solution running from $M_0(\sigma)$ to $M_1(\sigma)$, the ordering of $M_0(\sigma)$ and $M_1(\sigma)$, can be interchanged so that $D = \{M_0(\sigma), M_1(\sigma), M_a(\sigma)\}$ is also a Morse decomposition of $S(\sigma)$. Theorem 3.5 B with Lemma 3.4 B then implies that, if c is small, the connection map for the pair $M_1(\sigma)$, $M_a(\sigma)$ is trivial.

Now Lemma 3.4 C with Theorem 3.5 C and then 3.5 B implies that for large c, D is again a Morse decomposition but the connection map for the pair $M_1(\sigma)$, $M_a(\sigma)$ is no longer trivial: it is an isomorphism between the index of $M_a(\sigma)$ and the suspension of the index of $M_1(\sigma)$.

The latter is the product of $\bar{I}$ with a pointed one sphere (Theorem 3.5 C) and then a pointed two sphere (Theorem 3.5 B; cf. Theorem 2.4 B) the result is a pointed three sphere, so the isomorphism isn't trivial.

Now Theorem 3.1, p. 72, Ch. IV of [1] implies that $D(\sigma) = \{M_0(\sigma), M_1(\sigma), M_a(\sigma)\}$ cannot be a decomposition for all c; in view of 7.1 C, p. 40, Ch. III of [1], this means there is some value of c for which there is a solution connecting $M_0(\sigma)$ and $M_1(\sigma)$, and this completes the proof of Theorem 3.2 B except for the limit statements which are obvious.

3.7 Concluding remarks.

The equations from population genetics seem to be rich in attracting or hyperbolic critical manifolds: in the case of two loci the "linkage disequilibrium surface" is such a manifold if there is a positive probability of crossovers (and no selection). With several loci analogous statements are true ([4]).

In the simplest case of two loci and two alleles, the critical manifold of the "spatially independent" equations is two dimensional while that for the travelling waves is four dimensional. Therefore the analysis of an example is more difficult.

It is not just the increase of dimension that creates difficulty, though. (In fact, this does not have to be serious per se as the example 3.2 B, p. 73 Ch. IV of [1] shows.) The real difficulty comes because the travelling wave equations are no longer in a form that makes them automatically gradient-like (as they must always be in the case of one locus and two alleles no matter what the form of the g_{ij} is). (Gradient-like equations are discussed in §6, Ch. I of [1]).

Because the spatially independent equations always have a gradient form, the gradient-like character is present for very large c (cf. Lemma 3.3 C) but not for small c (cf. Lemmas 3.3 A and 3.3 B where the gradient-like character with respect to H made the treatment very simple).

Actually, the Laplacian term is also a gradient term and one might expect the sum of two gradients to be a gradient. The hitch is that the metric with respect to which the spatially independent equations are a gradient system is not the usual one (but rather one suited to the simplex).

In [14] the "non-gradient" aspects of a model from Ecology are circumvented. It is possible that similar methods might be used in special cases of the equations treated here.

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A generalized Morse index theory is used to study the existence of travelling wave solutions of a diffusion-reaction system of equations. The reaction system is assumed to be "close" to one which admits an attracting manifold of critical points. A scaling argument is used to see that the equations for travelling waves of the full system are then close to a system with a normally hyperbolic manifold of critical points.

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20. Abstract continued.

Standard perturbation theorems are already available to study the behavior of solutions of the "perturbed" system which lie near the critical manifold in terms of a (derived) system of "slow" equations on the manifold itself. Here, another such theorem, dealing with aspects of the system which can be described in terms of isolated invariant sets, is proved. Specifically, it states that isolated invariant sets of the slow equations correspond to isolated invariant sets of the full system, and that the Morse index of the latter set is an n-fold suspension of that of the former where n is the number of unstable normal directions.

These theorems are applied to a standard continuous space-time natural selection-migration model for a diploid organism when the selective strength is weak. The selection is assumed to be determined by a single locus at which the number of available alleles is arbitrary, and the critical manifolds are found in this case.

The perturbation theorem is applied to a system with only two alleles in a situation where the existance of a travelling wave for the slow equation has long been known. The conclusion is that the full system also admits a corresponding travelling wave. The index theory is of use because the travelling wave itself is part of an isolated invariant set.

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